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Zoological Research

Dynamic Distribution of Glycoconjugates During Oogenesis of *Atractomorpha sinensis*

LÜ Shu-min[1], XI Geng-si[1,*], ZHAO Zhuo[2], TANG Chao-zhi[3]

(1. *College of Life Science, Shaanxi Normal University, Xi'an* 710062, *China*;
2. *College of Life Science, Jilin Normal University, Siping* 136000, *China*;
3. *College of Life Science, He'nan Normal University, Xinxiang* 453007, *China*)

Abstract: The dynamic distribution of three different glycoconjugates in oocytes and follicle cells during the oogenesis of *Atractomorpha sinensis* were detected using biotin-labeled Peanut Agglutinin (PNA), Soy Bean Agglutinin (SBA) and Ulex Europaeus Agglutinin I (UEA-I) lectins. The results showed that during oogenesis there was no distribution of the UEA-I receptor. The receptors of PNA and SBA were found to be dependent on developmental stage and present different distribution patterns accordingly. The binding sites of the two lectins indicated the presence of different sugars (PNA for Galβ1,3GalNAc and SBA for GalNAc) and showed considerable variation during oogenesis. PNA and SBA receptors first appeared at the oocyte growth phase, the PNA receptors then disappeared gradually and the SBA receptors exhibited the greatest expression. At the early phase of yolk formation, PNA and SBA receptors were located just at the brim of ooplasm, which was the region of vitellin formation. However at the later phase of yolk formation, neither of the two receptors was detected. In the mature egg, PNA and SBA receptors were distributed again on the vitellin membrane and the eggshell. The two receptors were also widely distributed in the follicular cells, showing similar distribution variation to the oocytes. The results indicate that the change and modification of the two receptors may be greatly related to the growth of oocytes, the preparation for yolk formation, the differentiation of follicular cells and the maturation of oocytes. The glycoconjugates on the vitellin membrane probably play important roles in sperm and egg recognition. The two lectins bound moderately or strongly to the eggshell, which indicates that the eggshell of *A. sinensis* contains the GalNAc and Galβ1,3GalNAc glycoproteins.

Key words: *Atractomorpha sinensis*; Oogenesis; Glycoconjugates; Oocyte; Follicle cell

短额负蝗卵子发生过程中糖复合物的动态分布

吕淑敏[1], 奚耕思[1,*], 赵 卓[2], 唐超智[3]

(1. 陕西师范大学 生命科学学院, 陕西 西安 710062; 2. 吉林师范大学 生命科学学院, 吉林 四平 136000;
3. 河南师范大学 生命科学学院, 河南 新乡 453007)

摘要: 以生物素标记的凝集素(UEA-I、SBA、PNA)为探针, 利用凝集素组织化学方法对短额负蝗(*Atractomorpha sinensis*)卵子发生过程中滤泡细胞和卵母细胞内糖复合物的分布进行了定位研究。结果表明, 在卵子发生的各期滤泡细胞和卵母细胞中没有UEA-I受体的表达, SBA和PNA受体以不同的分布模式呈阶段性表达。两者首次出现于卵母细胞生长期, 随后PNA受体消失, SBA受体大量表达; 在卵黄形成期前期SBA受体和重新出现的PNA受体表达于卵黄颗粒形成部位, 卵黄形成期后期两者均为阴性表达; 成熟卵子中两种受体又以不同程度重新出现于卵黄膜。两种受体在滤泡细胞内均大量表达。提示, N－乙酰半乳糖胺和半乳糖－β－(1,3)半乳糖胺复合物的修饰和变化与卵母细胞的发育、卵黄物质的形成及滤泡细胞的增殖分化密切相关, 卵黄膜上的糖复合

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Foundation item: The Natural Science Foundation of Shaanxi (2005 C_1 25)
* Author for correcpondence(通讯作者): E-mail: xigengsi@snnu.edu.cn
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第一作者简介: 吕淑敏(1980－07), 女, 汉族, 安徽黄山人, 博士研究生, 研究方向为动物生殖与发育; E-mail: lsmlst1980@stu.snnu.edu.cn

物可能与精卵识别有关。

关键词：短额负蝗；卵子发生；糖复合物；卵母细胞；滤泡细胞
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Glycoproteins and other glycoconjugates present on the surface of many cell types have been identified and assigned many functions, including neural adhesion, cell matrix, immune response, fertilization and development. Many data suggest that the biological and functional diversity of glycoconjugates is directly generated by the sequence, chain length and branching points of the monosaccharides (Varki, 1993). Consequently the study of glycosylation has become much more important. Recently many investigations have focused on the biological function of glycoconjugates in the reproductive system, such as in the oogenesis of the dusky grouper (Mandich et al, 2002; Fang and Welsh, 1995), the differentiation of pyriform cells in lizards (Uliano et al, 2001; Andreuccetti et al, 2001), the recognition and fusion of gametes in chickens (Robertson et al, 2000) and in other mammalian species (Kitammura et al, 2003). Glycoconjugates have also been detected on the zona pellucida of mammalian oocytes and have been demonstrated to play a role in the development of oocytes, the activation of eggs and the process of fertilization (Parillo et al, 2005, 2003; Prisco et al, 2003; Kitammura et al, 2003; EI-Mestrah et al, 2001). Compared with the vertebrates, there has been much less investigation of insect glycoconjugates and only two species have been reported (*Drosophila* and *Acrida cinerea*). The insects differ from mammalian species in many aspects of oocyte development. This is especially true for the orthopteran insects as the panoistic ovarioles depend on the follicular cells rather than the nurse cells to provide nutrients and molecular messengers for oocyte development (Xi et al, 2005).

To investigate how the glycoconjugates carry out their biological function during the oogenesis of panoistic ovarioles of Orthoptera. We used the orthopteran insect *Atractomorpha sinensis* Thumberg and selected the commonly used lectins (UEA-I, SBA, PNA) as probes to detect the dynamic distribution of three different glycoconjugates during oogenesis.

1 Material and Methods

1.1 Tissue preparation

The fifth and sixth instar of female larvae and all stages of mature females were collected from the paddy-fields from a southern suburb of Xi'an city. The ovaries were dissected in insect physiological saline, immediately fixed in Bouin's solution for more than 24 h and then routinely dehydrated with alcohol and embedded in paraffin wax. The sections were cut at 7 μm and used directly in staining experiments.

1.2 Lectin histochemistry

The sections were routinely dewaxed in xylene and rehydrated by passing through a series of alcohols (100% - 70%). The sections then were put in 0.1% Trypsin at 37℃ for 10 mins and rinsed with Tris-buffer saline (TBS) three times (5 mins each time). They were then put in 3% H_2O_2 (V/V) for 10 min and rinsed with TBS three times. We then incubated them with biotin-lectins (Vector, America, see Tab. 1) at 37℃ for 1 h in a humidified light-safe chamber and rinsed with TBS three times, incubated them with 2 μg/mL avidin Horseradish Peroxidase (Huamei Biology Company, China) at 37℃ for 30 min and rinsed with TBS three times. Finally, these sections were stained with DAB-H_2O_2 and observed with an Olympus microscope.

1.3 Controls

The following controls were used: (1) substitution of the TBS buffer for the lectins; (2) preincubation of the lectins with the corresponding sugar inhibitor (0.2 mol/L, see Tab. 1) at 4℃ overnight and then applied to the sections as described above. The sugar specificities and the inhibiting sugars for the lectins used in this study are listed in Tab. 1.

1.4 Image collection and data processing

Five lectin-labeled sections from each stage were

Tab. 1 Concetration, specificity and inhibiting sugar for the lectins used

Origin of lectin	Acronym	Concentration (μg/mL)	Sugar specificity	Sugar inhibitor
Soybean Agglutinin	SBA	20	βGalNAc	GalNAc
Peanut Agglutinin	PNA	25	Gal β1,3GalNAc	Gal
Ulex Europaeus Agglutinin I	UEA-I	30	L-Fuc	L-Fuc

Fuc: fucose; GalNAc: N-acetylgalactosamine; Gal: galactose.

selected and put every section into HPIA S2100 high definition and colour picture analyzing system. The intensity of lectin staining was calculated by the grey value of the images. The mean grey value of different stage oocytes and follicular cells were automatically collected (all data was collected in 20× object lens). The data was then input into SPSS 13.0 software and analysed using one-way ANOVA with Dunnett's multiple comparison tests as appropriate.

2 Results

2.1 Results of PNA labeling

2.1.1 Distribution of PNA receptors on oocytes

PNA was positively labeled in the second, fifth and eighth stages of oocytes, and the grey value reflects those stages' differences (Tab. 2). A great deal of PNA receptors first appeared in the perinuclear region of the second stage of oocytes (Fig. 1B), which was the peak positive reaction, but the cell membrane also appeared and had a moderate positive reaction (arrow 1 in Fig. 1B). In the fifth stages of oocytes, there were only moderate positive marks at the brim of the ooplasm, which is the vitellin formation region (arrow 2 in Fig. 1F). The positive granules in the perivitelline space were also evident (arrow 1 in Fig. 1F). In the matured egg, the PNA receptors were located at the brim of the flaky yolk (arrow 1 in Fig. 1J) and the vitellin membrane and the eggshell appeared as a weak positive mark (Fig. 1J).

2.1.2 Distribution of PNA receptors on follicular cells

During the oogenesis, all stages of follicular cells were positive for PNA and the comparison of grey values is summarized in Tab. 2, briefly described below. The first and second stages of follicular cells had a moderate positive PNA mark (Fig. 1: A, B), and there was no distinct differences between the two stages (Tab. 2); In the third stage, positive reaction became stronger and was mainly distributed at the joint of follicular cells (Fig. 1C). In the fourth stage, the positive mark reached its peak and large positive granules were located at the region near the oocytes (arrows in Fig. 1: D, E). In the last four stages, the pattern of positive marks remained steady with a strong positive granule in the region near the oocytes (Fig. 1: F–J).

The control experiment showed a negative reaction (Fig. 1: A1–J1).

Tab. 2 The degree of PNA receptor positive reaction in different periods of oogenesis in *Atractomorpha sinensis*

Grey value of PNA	Oocytes	Follicular cells
Stage 1	–	$82.1000^{a} \pm 2.57099$
Stage 2	$74.1250^{a} \pm 3.14076$	$84.9000^{a} \pm 2.03005$
Stage 3	–	$64.7000^{b} \pm 2.20126$
Stage 4	–	$51.4000^{c} \pm 2.10924$
Stage 5	$97.7000^{b} \pm 2.88001$	$70.8000^{b} \pm 1.72434$
Stage 6	–	$80.2000^{a} \pm 1.63163$
Stage 7	–	$81.2000^{a} \pm 2.49355$
Stage 8	$90.1000^{c} \pm 1.99137$	$86.6000^{a} \pm 3.14183$

Means with different superscripts are statistically different, $P < 0.05$ (One-Way ANOVA, Two-tailed and Dunnett's multiple comparison).

2.2 Results of SBA labeling

2.2.1 Distribution of SBA receptors on oocytes The distribution pattern of SBA receptors in oocyte development was greatly different from that of PNA. All stages except for the first, sixth and seventh were positively marked for SBA, and the grey values of those stages were different (Tab. 3). A few positive granules first appeared in the perinuclear region of the oocytes (arrow in Fig. 2B). In the third stage, the positive granules in the perinuclear region increased and congregated into bigger granules (arrow in Fig. 2C). In the fourth stage, the positive granules diffused into the whole cytoplast of the oocytes (Fig. 2D), and reached the peak positive reaction in the late fourth stage (Tab. 3), the positive granules were greatly distributed around the brim of the cytoplast (Fig. 2E). In the fifth stage, a few positive granules were distributed at the brim of the ooplasm, which was the region of vitellin formation as previously described. The sixth and seventh stages showed negative reactions. In the matured egg, the vitellin membrane had a strong positive reaction and the eggshell a weak positive reaction (arrows in Fig. 2J).

2.2.1 Distribution of SBA receptors on follicular cells

The positive marks of SBA in all follicular cell stages were weaker than that of PNA. The grey value of every stage is summarized in Tab. 3. The first stage of follicular cells revealed moderate positive marks (Fig. 2A). The labeling gradually decreased in the second stage

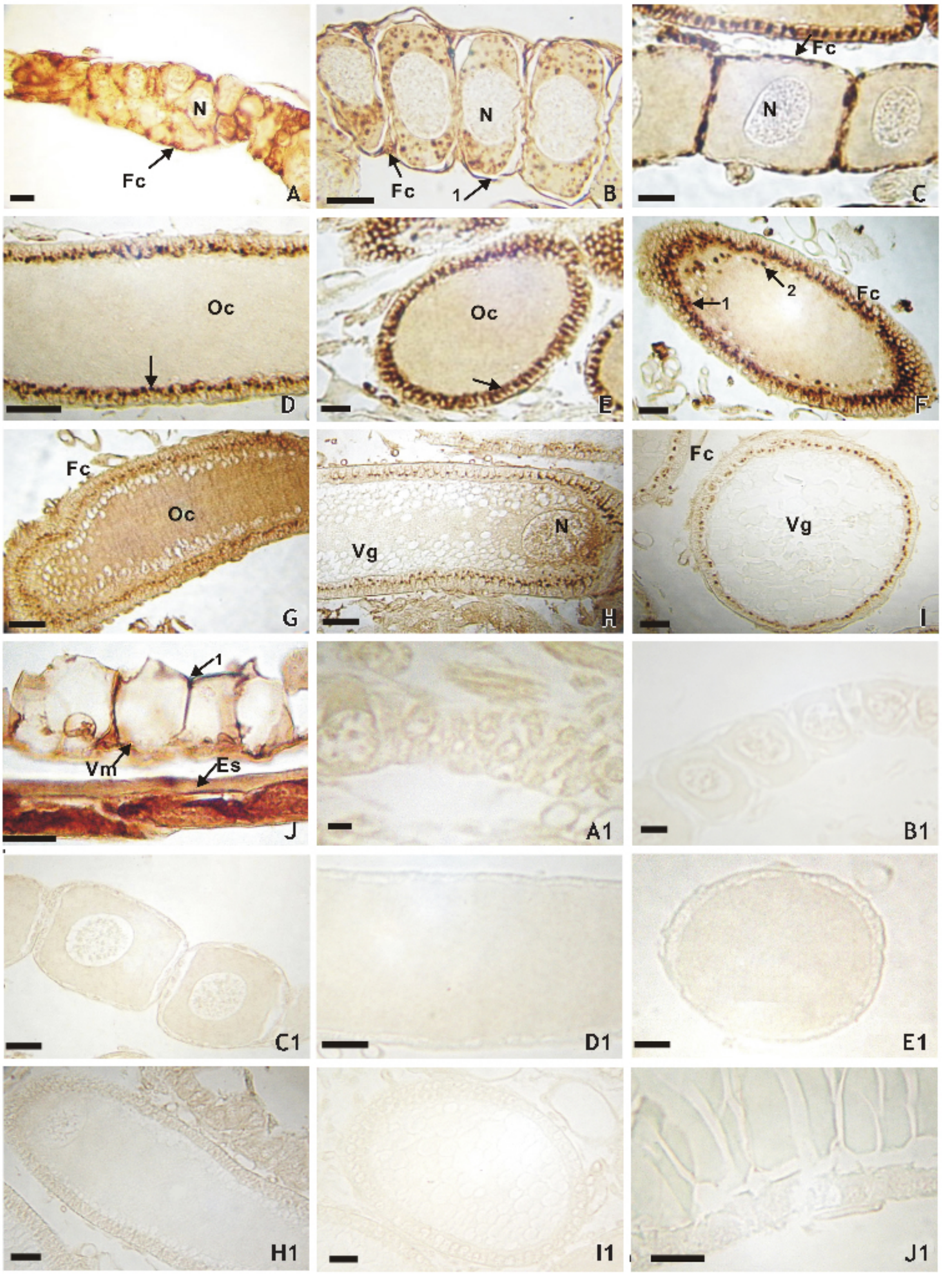

Fig. 1 The expression of PNA receptors during the oogenesis of *Atractomorpha sinensis*

A: The first stage of oogenesis, PNA labeling on the follicle cell; B: The second stage of oogenesis, PNA labeling on the oocyte and the follicle cell, arrow 1 showing the positive reaction on the membrane of oocyte. C: The third stage of oogenesis, PNA labeling on the follicle cell. D, E: The fourth stage of oogenesis, PNA labeling on the follicle cell; F: The fifth stage of oogenesis, arrow 1 showing PNA labeling on the perivitelline space; arrow 2 showing PNA labeling on the brim of the oocyte; G: The fifth stage of oogenesis, PNA labeling on the follicle cell; H: The sixth stage of oogenesis, one positive granule in the follicle cell; I: The eighth stage of oogenesis, positive reaction on the follicle cell, yolk membrane and egg shell, arrow 1 showing PNA labeling on the yolk; J: The seventh stage of oogenesis, one positive granule in the follicle cell. A1-J1 show negative reactions which are the controls of TBS and sugar competition.

Oc: Oocyte; Fc: Follicle cell; N: Nucleolus; Vg: vitellin granule; Vm: vitellin membrane; Es: Egg shell; Scale bar = 50 μm.

(Fig. 2B) and in the third and fourth stages, the positive marks increased. The SBA markings reached a peak in the fourth stage (Tab. 3) with the positive granules usually located at the joint of follicular cells (Fig. 2: C – E). There were moderate positive granules at the region near the oocytes in the fifth and seventh follicular cell stages (Fig. 2: F, G, I). The sixth stage showed a negative reaction. In the eighth stage,

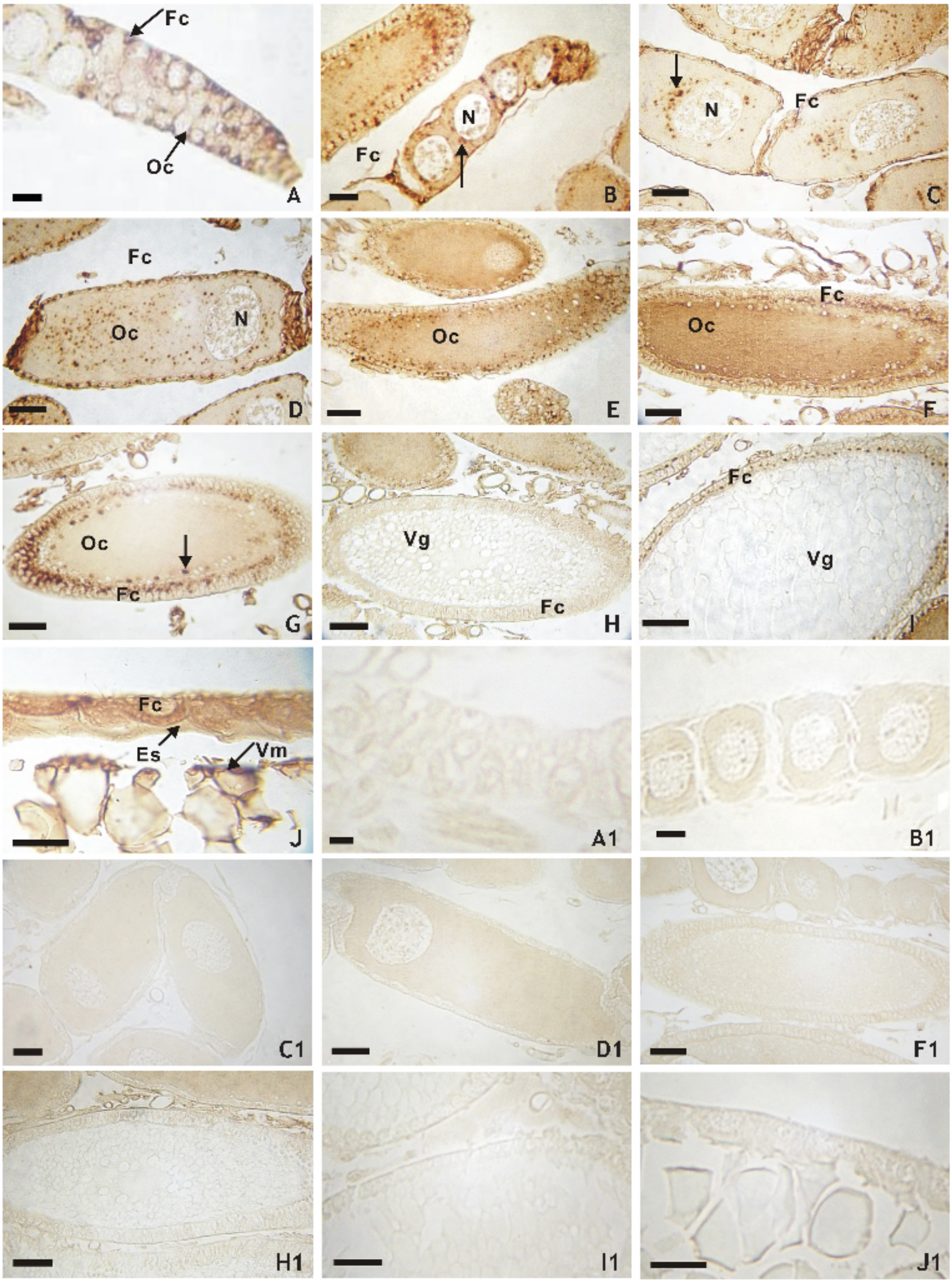

Fig. 2　The expression of SBA receptor during the oogenesis of *Atractomorpha sinensis*

A: The first stage of oogenesis, SBA labeling on the follicle cell; B: The second stage of oogenesis, SBA labeling on the oocyte and the follicle cell, arrow showing positive reaction around the brim of the nucleus of the oocyte. C: The third stage of oogenesis, arrow showing heavy reaction on the brim of the nucleus of the oocyte. D: The forth stage of oogenesis, SBA labeling on the follicle cell and oocyte. E: The late fourth stage of oogenesis, positive reaction on the brim of the oocyte cytoplasm. F: The fifth stage of oogenesis, SBA weakly labeling on the oocyte. G: The fifth stage of oogenesis, SBA labeling on the oocyte and follicle cell; H: The sixth stage of oogenesis, negative reaction on the oocyte and follicle cell. I: The seventh stage of oogenesis, one positive granule in the follicle cell. J: The eighth stage of oogenesis, weak positive reaction on the follicle cell and egg shell, heavy reaction on the yolk membrane. A1-J1: Negative reactions which are the controls of TBS and sugar competition.

Oc: Oocyte; Fc: Follicle cell; N: Nucleolus; Vg: vitellin granule; Vm: vitellin membrane; Es: Egg shell; Scale bar = 50 μm.

the degenerative follicular cells had a weak positive reaction (Fig. 2J).

The control experiment showed a negative reaction (Fig. 2: A1 – J1).

Tab. 3 The degree of SBA receptor positive reaction in different periods of oogenesis in *Atractomorpha sinensis*

Grey value of SBA	Oocytes	Follicular cells
Stage 1	-	$90.7000^a \pm 2.08193$
Stage 2	$81.1000^a \pm 2.33071$	$98.0000^b \pm 1.86786$
Stage 3	$70.8000^b \pm 2.78807$	$88.0000^a \pm 1.90321$
Stage 4	$62.3000^c \pm 3.60879$	$54.7000^c \pm 3.06974$
Stage 5	$103.2000^d \pm 2.18480$	$85.9000^a \pm 3.19531$
Stage 6	-	-
Stage 7	-	$89.6000^a \pm 1.98438$
Stage 8	$74.4444^e \pm 2.82406$	$117.1000^d \pm 3.68616$

Means with different superscripts are statistically different, $P < 0.05$ (One-Way ANOVA, Two-tailed and Dunnett's multiple comparison).

2.3 Comparison of intensity of the two lectin receptors

The data above were put into SPSS 13.0 software, and analysed using one-way ANOVA with Dunnett's multiple comparison tests. The grey value of two lectins in the same stages of oocytes and follicular cells were compared and the histograms calculated in Excel (Fig. 3 and Fig. 4).

3 Discussion

PNA, SBA and UEA all acted as markers for the presence or absence of sugars during the oogenesis of *Atractomorpha sinensis*, as outlined in Tab. 1. This study has therefore demonstrated that L-Fuc was absent during the process of oogenesis of *A. sinensis*, while the glycoconjugates, which contained GalNAc and Galβ1,3GalNAc, showed a grade-distribution and different distribution patterns in oocytes and follicular cells, respectively. They played an essential role in modulating oogenesis including the oocyte and follicular cell growth. The receptors of PNA and SBA first appeared moderately or strongly at the first follicular cell stage. At the second stage, the labeling mark of both lectins showed weaker than in the first stage, which may be related to the redistribution of the glycoconjugates from the multiplication of follicular cells. The PNA and SBA receptors increased greatly and reached peak values (Tab. 2, 3) in the fourth stage. Our study showed that the PNA and SBA receptors obviously changed and modified during the differentiation of follicular cells, and the positive granules were mainly located at the joints of follicular cells. These results demonstrated that GalNAc and Galβ1,3GalNAc may play an important role in modulating the growth and differentiation of follicular cells.

The Galβ1,3GalNAc on the membrane of follicular cells may relate to the information exchange between the oocytes and the lymphoid. At the beginning of vitellogenesis, there was a large positive granule of PNA and SBA in the region near the oocytes. Former investigations (Dou & Xi, 2003; Ouyang et al, 2005) showed that follicular cells in this stage were full of mitochondria, golgiosomes, endoplasmic reticulum (ER) and high intensity granules. These granules were similar to yolk granules and were also observed in the cytoplasm near the oocytes during the vitellogenesis of *Acrida cinerea*. In this regard, we speculated that the receptors of SBA and PNA may take part in yolk protein synthesis and the PNA receptors in the perivitelline space may either be secreted by the follicular cells or derived from the lymphoid. The SBA receptors in follicular cells underwent obvious changes during vitellogenesis. Moreover, in this phase the morphology of the follicular cells changed greatly. These results indicate that SBA receptors are related to the differentiation of follicular cells in the vitellogenesis phase. The PNA and SBA receptors showed high expression in the formation of the vitelline membrane, which suggests that GalNAc and Galβ1,3GalNAc play roles in the formation of the vitelline membrane. This finding is in agreement with former studies on some vertebrate species (Prisco et al, 2003; Chang et al, 2004). Also, the egg shell of insects is composed of the protein secreted by follicular cells. In our study, the PNA and SBA receptors on the egg shell demonstrated that the shell of *A. sinensis* contains GalNAc and Galβ1,3GalNAc glyproteins.

The result of lectin labelling of the oocytes showed that the receptors first appeared in the perinuclear region of the oocytes. And former studies on the oogenesis of *A. cinerea* also indicated that the mitochondria and ribosomes were distributed in the second stage of oocytes (Ouyang et al, 2005). Accordingly, we speculated that the GalNAc and Galβ1,3GalNAc glycoconjugates may be primarily synthesized by the oocytes themselves. Furthermore, the PNA receptors disappeared while the SBA receptors increased, which may be relat-

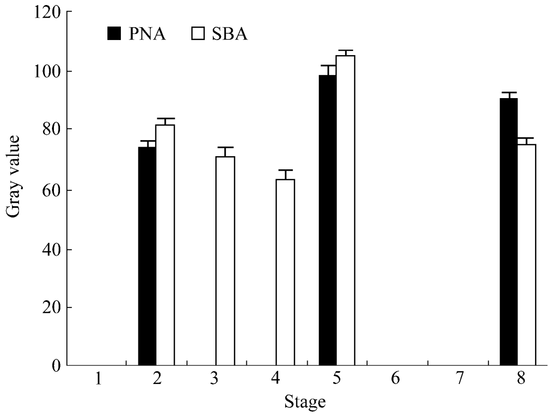

Fig. 3　The grey values of two receptors in different oocyte stages

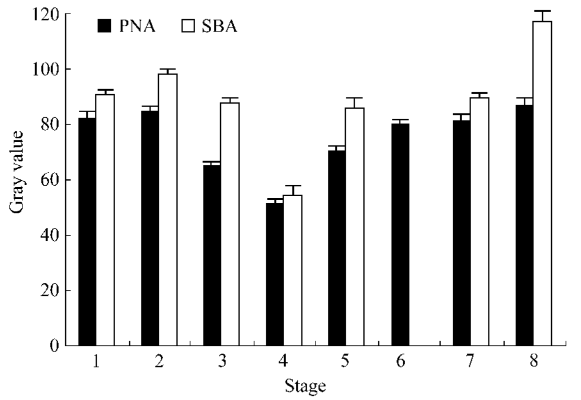

Fig. 4　The grey values of two receptors in different follicular cell stages

ed to the growth of the oocytes. During the fifth stage, the PNA receptors reappeared and were located with the SBA receptors at the region of vitellin formation in the vitellogenic oocytes. This indicates that the GalNAc and Galβ1, 3GalNAc residues probably take part in vitellogenesis, which is also supported by former studies on the oogensis of *A. cinerea* (Ouyang et al, 2005).

During the process of vitellogenesis, the two sugar residues underwent obvious changes and modifications (Tab. 2, 3). Glycosylation is very important for the structure and function of proteins. In the case of vitellin, a ubiquitous protein accumulated and became the main yolk protein of the oocytes. During oogenesis, glycosylation is crucial for the folding, processing and transporting of proteins to the yolk and also provides a source of carbohydrate during embryogenesis (Khalaila et al, 2004). This study showed that the changes and modifications of the two sugar residues during vitellogenesis probably contribute to the formation and transportation of yolk. Usually, the sperm-egg interaction is mediated by oligosaccharides of the zona pellucida; glycoconjugates may play great roles in the recognition and fusion of gametes and the fertilization and inhibition of cortical reactions for multiple sperm (Lee, 1998; Mandich et al, 2002; Prisco et al, 2003; Chang et al, 2004). In insects, the structure of the vitelline membrane is the same as the zona pellucida of mammals in many functions. Consequently, the GalNAc and Galβ1, 3GalNAc glycoconjugates on the vitelline membrane may play an important role in sperm and egg recognition.

In summary, the results demonstrated that during the oogenesis of *A. sinensis*, the development of the follicular cells and oocytes is accompanied by remarkable changes and modifications of glycoconjugates, which may be related to the growth and differentiation of these cells. Compared with former studies, it can be concluded that the distribution and function of glycoconjugates during oogenesis exhibits interspecies variation and development-period dependency. In vertebrates, more and more glycosylation mechanisms and crucial enzymes in carbohydrate metabolism have been identified. In comparison, in insects little is known about the glycosylation mechanisms, and the analysis of developmental changes in glycosylation has so far mostly relied on the use of lectins with specificity for specific sugar configurations (Fredieu & Mahowald, 1994; Callaerts et al, 1995). The location of the glycoconjugates is required, but analysis of the genes for the crucial enzymes in carbohydrate metabolism is also required at a molecular level.

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国家自然科学基金委“第七届生命科学学术研讨会”在昆明召开

由国家自然科学基金委主办，中国科学院昆明动物研究所和云南大学承办的“第七届生命科学学术研讨会暨国家杰出青年科学基金研究进展报告会”于 11 月 6 日在昆明经贸宾馆开幕。

中国科学院昆明动物研究所所长张亚平院士主持开幕式，国家自然科学基金委副主任朱作言院士，国家自然科学基金委生命科学部常务副主任杜生明研究员，云南省科技厅副厅长王建华，中国人民解放军第三军医大学吴玉章教授，云南大学副校长张克勤研究员分别在开幕式上致词。国家自然科学基金委生命科学部副主任冯雪莲研究员做了“生命科学部国家杰出青年基金资助工作报告”。张启发院士、沈岩院士、杨焕明研究员、武维华研究员和徐林研究员分别应邀在大会上作了学术报告。

会议进行了 5 天，分别在在昆明和丽江举行。来自全国各地的约 150 生命科学领域的杰出青年基金获得者交流了各自的研究成果和在基金项目中的研究进展。

国家自然科学基金委“生命科学学术研讨会暨国家杰出青年科学基金研究进展报告会”每两年举办一次，是国内生命科学最高水平的学术会议，只有国家杰出青年科学基金的获得者才能参加。参加者在各自的学科研究领域里成绩优异。

（中国科学院昆明动物研究所 计财处，云南 昆明 650223）